

A NEW ARABELLID POLYCHAETE LIVING IN THE MANTLE CAVITY OF DEEP-SEA WOOD BORING BIVALVES (FAMILY PHOLADIDAE)

Harlan K. Dean

Abstract.—A new species of polychaete, *Pholadiphila turnerae* (Family Arabellidae), is described from the mantle cavity of two species of wood boring bivalves (Family Pholadidae, Subfamily Xylophagainae). This is the first reported association between an arabellid polychaete and a mollusk. This species shows reductions in jaw structure and setal development similar to the reductions observed in many endoparasitic arabellids. The jaw apparatus consists of three pair of maxillae, a short, slender maxillary carrier, and well-developed mandibles. Setae are of three types: acuminate, capillary and spinous. Ecological aspects of commensal/parasitic polychaetes living in a bivalve mantle cavity are discussed.

Woody plant material washed into the deep sea is rapidly decomposed by wood boring bivalves of the family Pholadidae, subfamily Xylophagainae, and acts as a center for organic enrichment communities at abyssal depths (Turner 1973, 1977, 1981; Wolff 1976; Grassle 1987). As part of a long-term study of these communities by Dr. Ruth Turner, the DSRV *Alvin* has been utilized to place "wood islands" and associated wood panels in the deep sea and recover them after varying periods of time. While studying the polychaetes associated with the recovered wood panels, several specimens were encountered living in close association with the wood boring bivalve mollusks. Specimens of two members of the subfamily Xylophagainae (Family Pholadidae), *Xyloredo ingolfia* Turner, 1972 and an as yet undescribed genus and species (Turner, pers. comm.) were found to harbor a previously undescribed species of Arabellidae within their infrabranchial chamber (Fig. 3A). This paper describes the arabellid species, *Pholadiphila turnerae*, and discusses its ecology.

Family Arabellidae Hartman, 1944
Pholadiphila, new genus

Diagnosis.—Body slender, elongate, flattened dorso-ventrally, segmentation distinct. Prostomium small, conical, antennae and palps absent, eyespots lacking. Prostomium indistinctly separate from the first segment. Peristomial ring indistinct. Three pairs of equal maxillae; MI falcate, bifid; MII ctenoid with appressed, blade-like processes; MIII small avicular. Maxillary carrier short, slender tripartite anteriorly. Mandibular plates large, smooth, shield-like; united medially. Parapodia uniramous, conical, cirri absent. Setae simple, 3 types: stout, emergent spines (Fig. 3C); more slender acuminate setae (Fig. 3D); and capillary setae (Fig. 3B).

Remarks.—The Arabellidae Hartman, 1944 and Oeononidae Kinberg, 1865 (emended by Colbath 1989a) are separated from other eunicoids by their prionognath jaw pattern and the possession of unmineralized jaws (Colbath 1989a). The prionognath jaw pattern is characterized by two long, slender maxillary carriers and what is usu-

ally termed a ventral "third carrier" (or ligament by Colbath [1986]). Three genera of predominantly endoparasitic arabellids are exceptional in that the maxillary carriers are fused along much of their length while the third carrier may (*Haematocleptes* Wirén, 1886, *Labrorostratus* Saint-Joseph, 1888) or may not (*Oligognathus* Spengel, 1882) be evident. The possession of a slender maxillary carrier with indications of a tripartite anterior end (Fig. 2E) by *Pholadiphila turnerae* strongly suggests fusion of what was originally a prionognath maxillary carrier pattern. The reduced number of maxillae and the fused, short (but not broad) maxillary carrier are believed to be the consequence of a commensal or parasitic lifestyle similar to the jaw reductions seen in other parasitic genera within the Arabellidae. The small jaw apparatus of *P. turnerae* is a translucent amber structure showing no indication of the mineralization seen in labidognath jaws, again in agreement with the prionognath jaw type.

In addition to jaw structure, several other characteristics associate *P. turnerae* with the family Arabellidae. Arabellids are characterized as having a cylindrical body of nearly uniform width, a reduced prostomium lacking appendages and uniramous parapodia (Hartman 1944). Members of the Oeonidae Kinberg, 1865 (emended by Colbath 1989a), which also have prionognath jaws, differ from *P. turnerae* in the possession of one to three antennae, elongate postsetal lobes, prominent dorsal cirri, and geniculate setae (Colbath 1989a).

Hartman (1944) described the Arabellidae as possessing simple, limbate setae sometimes accompanied by projecting acicular spines (or ventral setae [Colbath 1989b]). Capillary setae have also been described for some of the parasitic species of Arabellidae (Pettibone 1957). The thick emergent spines and capillary setae of *P. turnerae* are both compatible with its inclusion within the Arabellidae. The characteristic limbate setae are absent in this species,

probably due to setal modifications correlated with its lifestyle. Similar reductions in setae have generally been associated with commensalism in the Polychaeta (Blake 1990) and with parasitism in other members of the Arabellidae (Pettibone 1963, Uebelacker 1984).

Pholadiphila turnerae, new species

Figs. 1–3

Material examined.—WHOI Deep Ocean Station No. 2: 38°17.5'N, 69°35.2'W, 3602 m. Wood Panel N-30; submerged 5 Sep 1975 (*Alvin* Dive 601), recovered 23 Sep 1977 (*Alvin* Dive 790): HOLOTYPE (USNM 145086) removed from the infrabranchial cavity of *Xyloredo ingolfia* Turner 1972 (Family Pholadidae). Paratype (USNM 145087) specimen with anterior end extending out of the exhalent siphon of a pholad belonging to an undescribed genus of the subfamily Xylophagainae. Paratype (MCZ 20008) specimen with anterior end extending out of the excurrent siphon of a pholad belonging to an as yet undescribed genus of the subfamily Xylophagainae. Wash material from recovery box carrying panels N-30 and N-42; panels submerged 5 and 6 Sep 1975 (*Alvin* Dives 601 and 602, respectively), recovered 23 Sep 1977 (*Alvin* Dive 790): Paratype (USNM 145089). Wood Panel N-83; submerged 23 Sep 1977 (*Alvin* Dive 790), recovered 3 Aug 1980 (*Alvin* Dive 1031): Paratype (USNM 145088). WHOI Deep Ocean Station No. 1, 39°45.3'N, 70°41.2'W, 1767 m. Wood Panel N-68; submerged 17 Aug 1976 (*Alvin* Dive 685), recovered 29 Jul 1977 (*Alvin* Dive 773): Paratype (MCZ 20009).

Description.—Specimens, preserved in alcohol, light yellow to buff. Body long and slender (Fig. 1A), flattened ventrally and weakly arched dorsally. Body tapered anteriorly from about setiger 10, sides parallel for most of body, tapered near the posterior end. Holotype 163 setigers, 15.4 mm long with maximum width 0.23 mm excluding

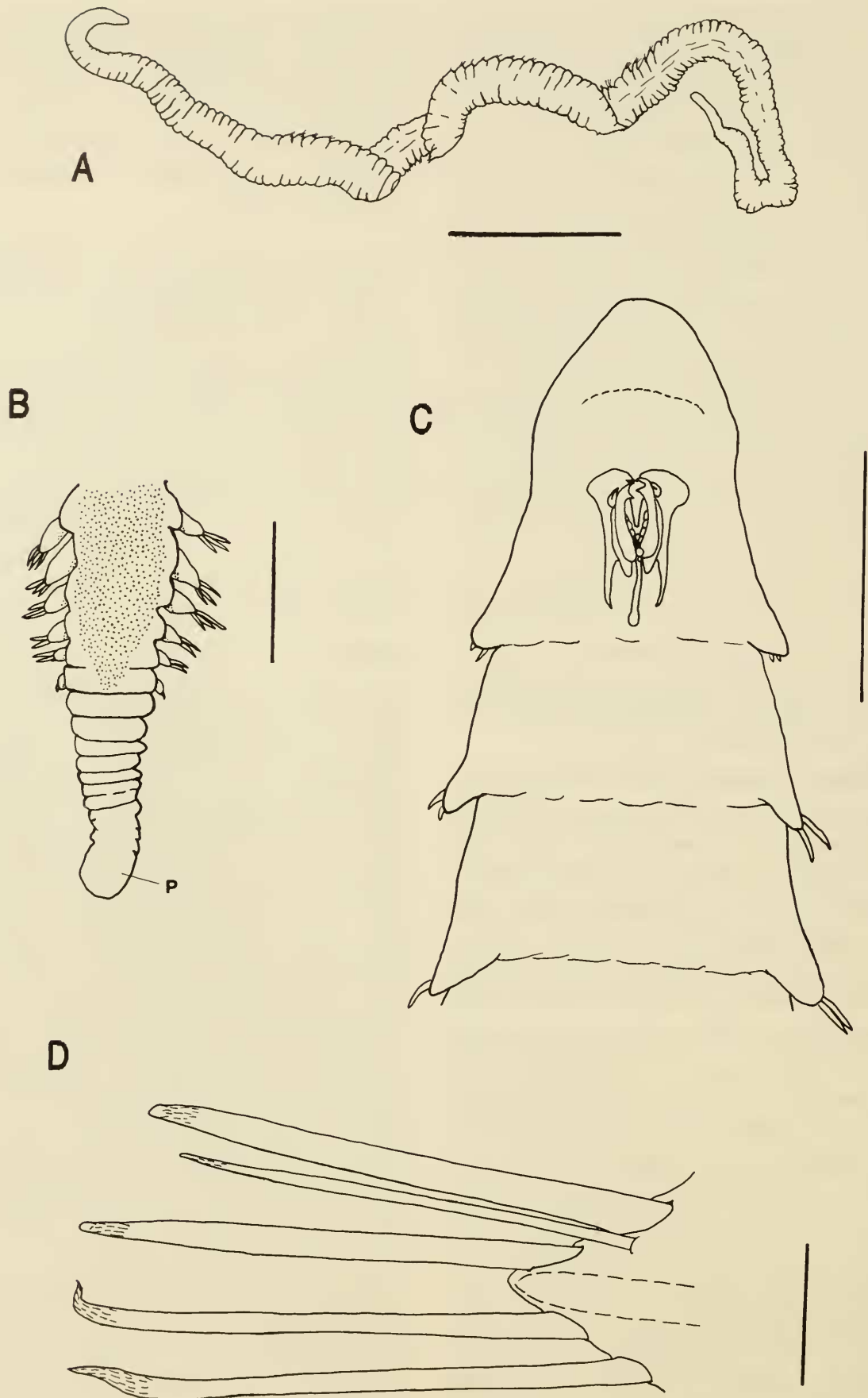


Fig. 1. *Pholadiphila turnerae*: A, Entire worm, holotype USNM 145086, anterior end on the left and the body has been twisted several times (Scale bar = 1.0 mm); B, Pygidial region, P = pygidium (Scale bar = 200 μ m); C, Anterior end (Scale bar = 100 μ m); D, Median parapodia, anterior view (Scale bar = 20 μ m).

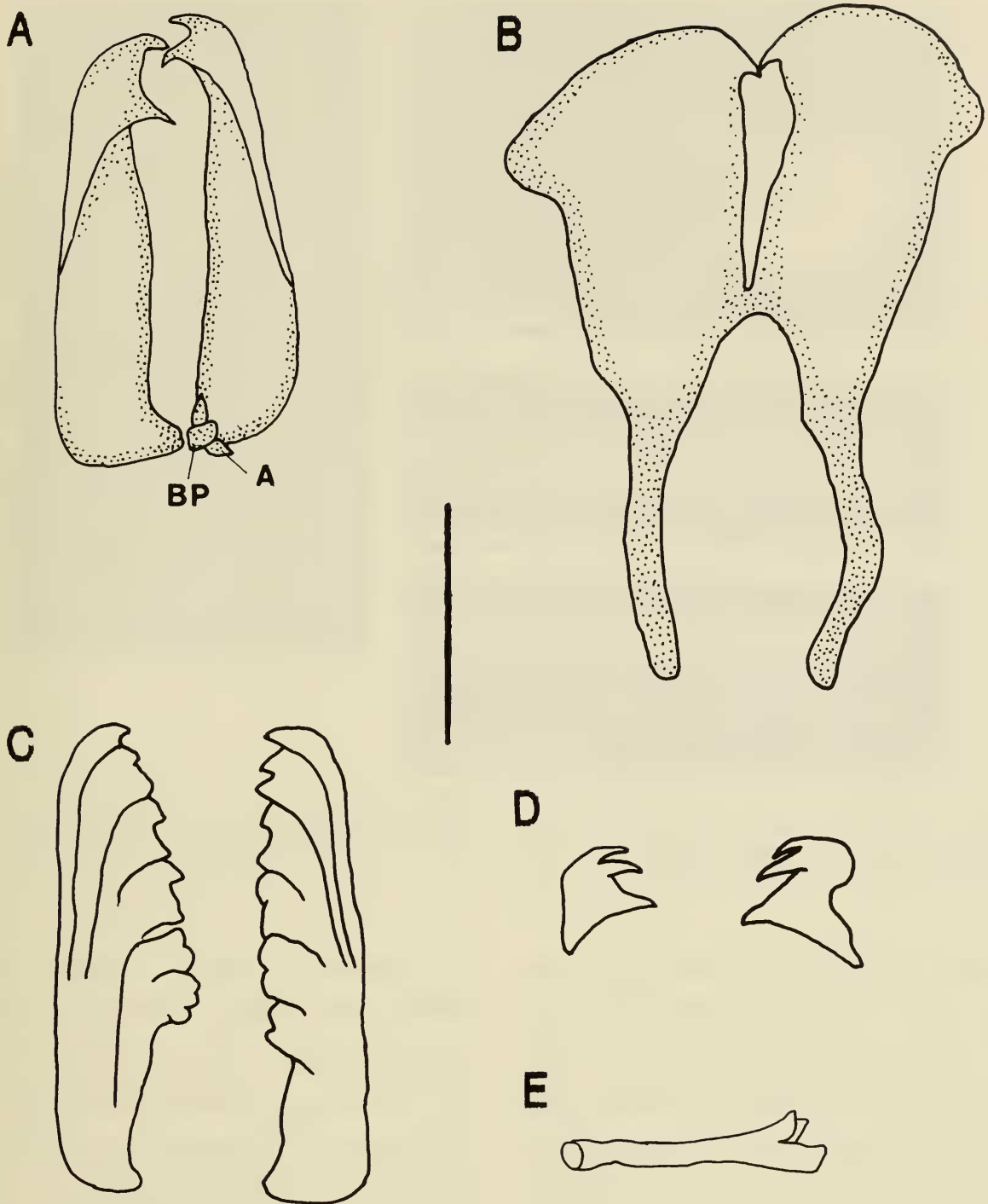


Fig. 2. Jaw apparatus of *Pholadiphila turnerae* drawn from a squash preparation of paratype MCZ 20009: A, Maxillae I, BP = basal plate, A = alae; B, Mandibles; C, Maxillae II; D, Maxillae III; E, Maxillary carrier (Scale bar = 20 μ m).

parapodia. Largest specimen examined 262 setigers, 19.2 mm long with maximum width 0.27 mm excluding parapodia. Prostomium conical, indistinctly separated from setiger 1, antennae, palps, and eyespots absent (Fig. 1C). Prostomium and peristomium fused.

Cuticular jaw apparatus: 3 pairs of max-

illae; MI gracile falcate, bifid with a pronounced gap between the falx and the smooth base (Fig. 2A), MIR with a thickened low cylindrical boss (basal plate, sensu Wolf 1980) possessing a pair of short alae; MII with 6 appressed, blade-like processes, 5 posterior with a pair of low bosses on the

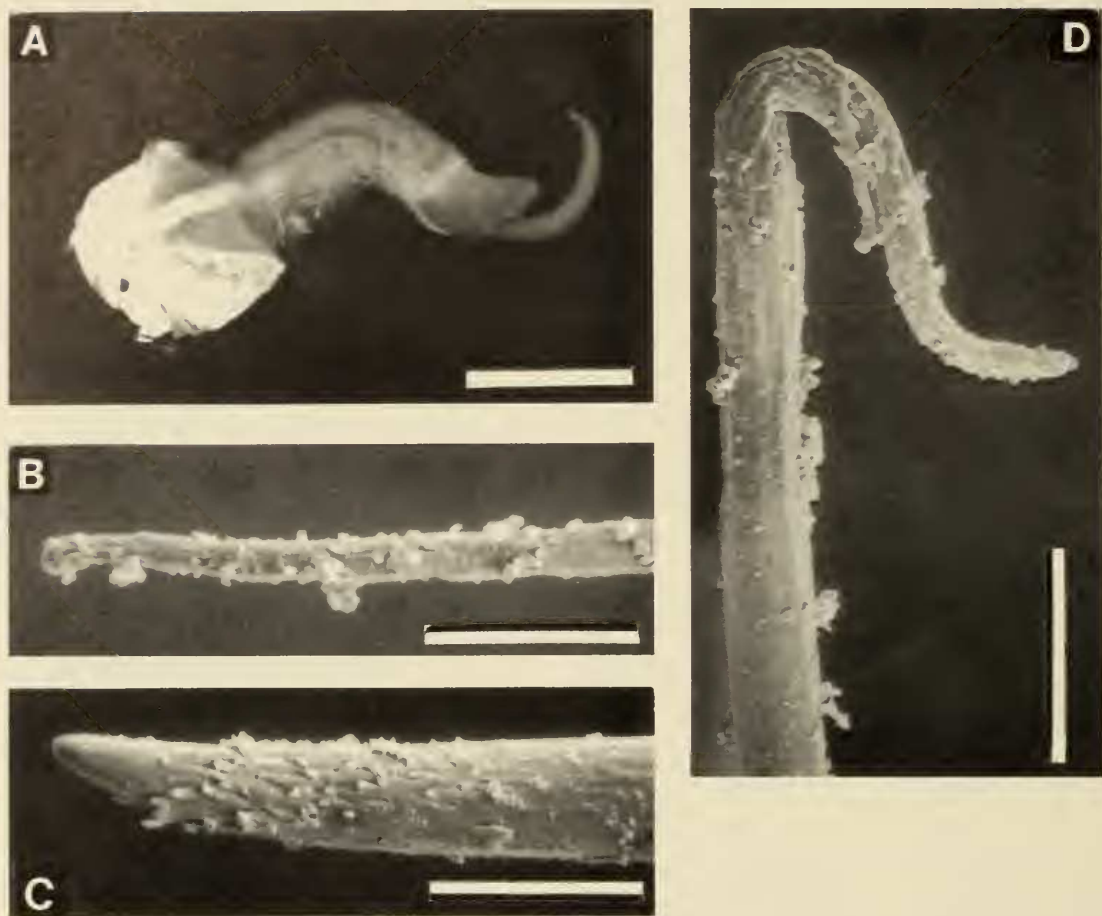


Fig. 3. *Pholadiphila turnerae*: A, paratype USNM 145087 with its anterior end extending from the siphonal opening of a specimen of an undescribed Xylophaginae (Family Pholadidae), most of the body may be seen coiled within the branchial chamber of the pholad (Scale bar = 1.0 mm); B, Capillary seta; C, Stout, emergent spine; D, Acuminate seta (Scale bars B–D = 5 μ m).

medial border, basal portion unarmed, extending posterior to the base of MI (Fig. 2C); MIII small, avicular, with wide base and 2 sharply pointed teeth (Fig. 2D). Maxillary carrier slender, short (shorter than MI sensu Colbath 1989b), cylindrical, recurved, anterior with a pair of dorsal bosses and a single ventral extension (Fig. 2E). Mandibles a pair of large flat plates united postero-medially; anterior border of each plate slightly convex with single weak tooth at antero-medial margin (Fig. 2B); each mandible with a slightly curved, free end approximately equal in length to the plate.

Parapodia conical, with single stout acicula (Fig. 1D); with 1 stout spine (Fig. 3C) and a small, supra-acicular capillary seta (often broken) on setiger 1; 2 stout, supra-acicular spines on setiger 2; 2 supra-acicular

stout spines and capillary seta (Fig. 3B) beginning on setiger 3; a stout, sub-acicular spine added at setiger 10; 2 stout, supra-acicular spines, a supra-acicular capillary seta and 2 sub-acicular acuminate setae (Fig. 3D) beginning at setiger 19 or 20 (the superior acuminate seta formed by transformation of one of the stout spines with intermediates occurring on setigers 18 and 19) and continuing to the pygidial region. Final setiger with two short, supra-acicular spines; 2 preceding setigers with 2 stout, supra-acicular spines and a sub-acicular, acuminate seta. Capillary and acuminate setae hirsute throughout, stout spines weakly hirsute posterior to setiger 20 (Fig. 3B–D). Posterior region with 7 (9 in the largest specimen examined) distinct, asetigerous segments and an undifferentiated cylindrical region ante-

rior to the pygidium; anus terminal (Fig. 1B).

Etymology.—This species is named in honor of Dr. Ruth Turner in recognition of both her extensive work with the wood boring bivalve mollusks and the support and encouragement she has shown me.

Remarks.—In some respects *Pholadiphila turnerae* has a less reduced jaw apparatus than many of the parasitic genera in the Arabellididae. The well-developed, diamond-shaped mandibular plates that are fused along part of their length are similar to the mandibles of free-living arabellids. In the genera *Labrorostratus*, *Haematocleptes* and *Oligognathus* the mandibles are reduced to small plates and they are entirely absent in the parasitic species of *Drilonereis* Claparède, 1870. The 3 pairs of well-developed maxillae (MI falcate, MII and MIII toothed) of *P. turnerae* are most similar to those of the parasitic species of the genus *Drilonereis* that possess 4 pairs of maxillae and to those of the free-living arabellids which possess 5 pairs of well-developed maxillae. In the remaining parasitic genera, the maxillae of *Oligognathus* have been reduced to 3 pair of unidentate hooks while those of *Labrorostratus* and *Haematocleptes* have been reduced to 2 pair of small cuticular pieces.

Whereas the maxillae of *P. turnerae* are less reduced than those of several parasitic arabellids, its maxillary carriers are greatly modified. Free-living arabellids and both free-living and parasitic members of the genus *Drilonereis* possess a pair of long, slender maxillary carriers with a third carrier attached ventrally. The paired maxillary carriers have been fused in *Labrorostratus*, *Haematocleptes* and *Oligognathus* with the third carrier retained in the former two genera and lost in *Oligognathus*. The maxillary carriers of *Pholadiphila turnerae* are fused along their entire length and the ventral extension may represent a vestigial third carrier. There is also a size reduction in the

maxillary carrier of *P. turnerae* being approximately equal in length to the maxillae while those of all other arabellids are much longer than the maxillae.

Reductions in the arabellid setal pattern are seen in the parasitic species *Drilonereis benedicti* Pettibone, 1957 which has no emergent setae and in the two species of the genus *Haematocleptes*, *H. terebellidis* Wirén, 1886 and *H. leaenae* Hartman & Fauchald, 1971, which possess slender, distally pointed setae rather than limbate setae. The setal arrangement of *Pholadiphila turnerae* agrees with that of the above mentioned species as all other members of the arabellids (parasitic or free-living) possess limbate setae with a well-developed blade (sensu Colbath 1989a). The acuminate setae and the strong spines of *P. turnerae* may be an adaptation to the parasitic or commensal existence of this species, affording strong purchase against the body of its molluscan host. These setae are more highly developed than the setae seen in other parasitic arabellids being more robust, more numerous and extending out much further from the parapodia.

Ecology.—Endoparasitism among the Polychaetes is known to occur almost exclusively in members of the family Arabellidae. A review of the known endoparasitic arabellids (review by Pettibone 1957, Day 1960, Hartman & Fauchald 1971, Emerson 1974, Amaral 1977, Uebelacker 1978, Wu et al. 1982, San Martín & Sardá 1986) reveals that, with the exception of *Oligognathus bonelliae* Spengel, 1882 (found living within the body cavity of the Echiuroid *Bonellia viridis* Rolando), all the known arabellid parasites have been found within the body cavity or gut (in the case of *Haematocleptes terebellidis*) of polychaete hosts. *Pholadiphila turnerae* is unlike most of the parasitic arabellids in that it lives external to the host's body cavity (within its mantle cavity) and is the first arabellid reported to form an association with a mollusk.

It is not clear if the association between *P. turnerae* and the wood boring bivalves is commensal or parasitic. If the polychaete utilizes the host's mantle cavity simply as a refuge from predators (as Pettibone [1984] suggested may be true of the Polynoidae found in the mantle cavity of deep-water seep and vent mussels), then this would be an example of commensalism. There are several indications, however, that this association is actually a parasitic one. The mouthparts of *P. turnerae* are reduced in a similar manner to those of other arabellids known to be parasitic and argues for reliance upon a host for nutrition. Possible food sources within the pholad mantle cavity are the gill filaments, the mucus coat on these filaments, or perhaps partially digested material within the pholads wood storing caecum. The mere presence of such a large organism in the mantle cavity (Fig. 3A) may impede water flow to such an extent that a significant stress is placed upon the pholad host. If this is the case then this association must be considered a parasitic (parasite lives at the expense of its host) rather than a commensal (host is unaffected by the associated species) relationship.

Despite a large sampling effort in shallow waters, there have been few reports of polychaetes living as commensals or parasites within the mantle cavity of bivalve mollusks. A specimen of the syllid *Parasyllidea humesi* Pettibone, 1961 was reported from the mantle cavity of the intertidal bivalve *Tellina nymphalis* Lamark, however this must be considered as a fortuitous association because only one of the approximate 200 specimens of this polychaete collected by Pettibone (1961) was found within the bivalve, the remainder were free-living. The polychaete *Antonbruunia viridis* Hartman & Boss, 1965 (Family Antonbruunidae) has been described as a commensal in the mantle cavity of the bivalve *Lucina fosteri* Hartman & Boss, 1965 collected in 68–82.3 m off Madagascar. To date this is the only report of a polychaete species collected exclu-

sively from the mantle cavity of a shallow water bivalve host.

With greater sampling effort in the deep sea close associations between polychaetes and bivalves are being noted with increasing frequency. Pettibone (1984, 1986) has described two species of Polynoidae living within the mantle cavity of mytilid mussels from both the Galapagos Rift hydrothermal vents and the Florida Escarpment methane seeps. Three species belonging to a recently described family, the Nautiliniellidae Miura & Laubier, 1989 (emended by Miura & Laubier [1990]), have been described from Japanese cold-seeps living within the mantle cavities of two species of *Calypptogenia* and a species of *Solemya*. Blake (1990) has also described a fourth species of Nautiliniellidae from the Laurentian Fan in the Western North Atlantic (3800–3900 m) living in the mantle cavity of *Thyasira insignis*. *Pholadiphila turnerae* is yet another example of a deep-sea polychaete which has taken up existence within a bivalve mantle cavity. The presence of commensal/parasitic polychaetes in the bivalve mantle cavity seems more common in the deep sea than in shallow water environments.

Acknowledgments

The pholads were collected, dissected from wood panels, and the photographic work carried out as part of R. D. Turner's studies of deep-sea wood-boring communities supported by the Office of Naval Research, Contract no. N00014-84-0258 with Harvard University. The SEM pictures were taken by R. Pinto (Museum of Comparative Zoology, Harvard University) and A. Coleman (Museum of Comparative Zoology, Harvard University) did the photographic work. J. Carpenter (Organismal and Evolutionary Biology, Harvard University) provided the use of photomicrographic equipment. Insightful review by B. Hilbig (Science Applications International Corporation, Woods Hole) improved an early

draft of this manuscript. R. D. Turner (Harvard University) confirmed the identities of the pholads and both she and J. Blake (Science Applications International Corporation, Woods Hole) reviewed the manuscript.

Literature Cited

- Amaral, A. C. Z. 1977. Um poliqueto endoparasitico, *Labrorostratus prolificus* sp. nov., em nereídea.—Boletim do Instituto Oceanográfico, San Paulo 26:285–292.
- Blake, J. A. 1990. A new genus and species of polychaeta commensal with a deep-sea thyasirid clam.—Proceedings of the Biological Society of Washington 103:681–686.
- Claparède, E. 1870. Les Annélides Chètepodes du Golfe de Naples. Troisième partie.—Mémoires de la Société de Physique et d' Histoire naturelle de Genève 20(2):365–542.
- Colbath, G. K. 1986. Jaw mineralogy in eunican polychaetes (Annelida).—Micropaleontology 32:186–189.
- . 1989a. Revision of the family Lysaretidae, and recognition of the family Oeonidae Kinberg, 1865 (Eunicida: Polychaeta).—Proceedings of the Biological Society of Washington 102:116–123.
- . 1989b. A revision of *Arabella mutans* (Chamberlin, 1919) and related species (Polychaeta: Arabellidae).—Proceedings of the Biological Society of Washington 102:283–299.
- Day, J. H. 1960. The polychaete fauna of South Africa. Part 5. Errant species dredged off Cape coasts.—Annals of the South African Museum 45(3):261–373.
- Emerson, R. R. 1974. A new species of polychaetous annelid (Arabellidae) parasitic in *Diopatra ornata* (Onuphidae) from Southern California.—Bulletin of the Southern California Academy of Sciences 73:1–5.
- Grassle, J. F. 1987. Macrofaunal colonization of disturbed deep-sea environments and the structure of deep-sea benthic communities.—Deep-Sea Research 34:1911–1950.
- Hartman, O. 1944. Polychaetous annelids. Part V. Eunicia.—Allan Hancock Pacific Expedition 10:1–339.
- , & K. J. Boss. 1965. *Antonbruunia viridis*, a new inquiline annelid with dwarf males, inhabiting a new species of pelecypod, *Lucina fosteri*, in the Mozambique Channel.—Annals & Magazine of Natural History, ser. 13,8:177–186.
- , & K. Fauchald. 1971. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. Part 2.—Allan Hancock Monographs in Marine Biology 6:1–327.
- Kinberg, J. G. H. 1865. Annulata nova.—Öfversigt of Svenska Kongliga Vetenskaps-Akademiens Förhandlingar 21:559–574.
- Miura, T., & L. Laubier. 1989. *Nautilina calyptogenicola*, a new genus and species of parasitic polychaete on a vesicomid bivalve from the Japan Trench, representative of a new family Nautilinidae.—Zoological Science 6:387–390.
- , & ———. 1990. Nautiliniellid polychaetes collected from the Hatsushima cold-seep site in Sagami Bay, with descriptions of new genera and species.—Zoological Science 7(2):319–325.
- Pettibone, M. H. 1957. Endoparasitic polychaetous annelids of the family Arabellidae with descriptions of new species.—Biological Bulletin 113:170–187.
- . 1961. New species of polychaete worms from the Atlantic Ocean, with revision of the Dorvilleidae.—Proceedings of the Biological Society of Washington 74:167–186.
- . 1963. Marine polychaete worms of the New England Region. I. Aphroditidae through Trochochaetidae.—U.S. National Museum Bulletin 227:1–356.
- . 1984. A new scale-worm commensal with deep-sea mussels on the Galapagos hydrothermal vent (Polychaeta: Polynoidae).—Proceedings of the Biological Society of Washington 97:226–239.
- . 1986. A new scale-worm commensal with deep-sea mussels in the seep-sites at the Florida Escarpment in the Eastern Gulf of Mexico (Polychaeta: Polynoidae: Branchipolynoidae).—Proceedings of the Biological Society of Washington 99:444–451.
- Saint-Joseph, Baron de. 1888. Les annélides polychètes des côtes de Dinard. Part 2.—Annales des Sciences Naturelles, Paris, Série 7(5):141–338.
- San Martin, G., & R. Sardá. 1986. Sobre la presencia de un Arabélido (Polychaeta: Arabellidae) parásito de Silidos (Polychaeta: Syllidae), del género *Labrorostratus* en las costas españolas.—Boletín de la Real Sociedad Española de Historia Natural (Biologica) 82(1–4):141–146.
- Spengel, J. N. 1882. *Oligognathus bonelliae*, eine schmarotzende Eunicée.—Mitteilungen aus der Zoologischen Station zu Neapel 3:15–52.
- Turner, R. D. 1972. *Xyloredo*, a new teredinid-like abyssal wood-borer (Mollusca, Pholadidae, Xylophaginae).—Breviora 397:1–19.
- . 1973. Wood-boring bivalves, opportunistic species in the deep sea.—Science 180:1377–1379.
- . 1977. Wood, Mollusks, and deep-sea food

- chains.—Bulletin of the American Malacological Union 1977:13–19.
- . 1981. “Wood Islands” and the “Thermal Vents” as centers of diverse communities in the deep sea.—The Soviet Journal of Marine Biology 7(1):1–9.
- Uebelacker, J. M. 1978. A new parasitic polychaetous annelid (Arabellidae) from the Bahamas.—Journal of Parasitology 64:151–154.
- . 1984. Family Arabellidae Hartman, 1944. Pp. 1–29 in J. M. Uebelacker and P. G. Johnson, eds., Taxonomic guide to the Polychaetes of the Northern Gulf of Mexico. Final Report to the Minerals Management Service. Contract 14-12-001-29091. Barry A. Vittor & Associates, Inc., Mobile, Alabama. Vol. 6, chapter 42.
- Wirén, A. 1886. *Haematocleptes terebellidis*, nouvelle annélide parasite de la famille des Euni-
ciens.—Bihang till Kongliga Svenska vetenskapsakademiens Handlingar 11(12):3–10.
- Wolf, G. 1980. Morphologische Untersuchungen an den Kieferapparaten einiger rezenter und fossiler Eunicoidea (Polychaeta).—Senckenbergiana Maritima 12:1–182.
- Wolff, T. 1976. Utilization of seagrass in the deep sea.—Aquatic Biology 2:161–174.
- Wu, B. L., R. Sun, & D. Yang. 1982. On the occurrence of endoparasitic polychaetous annelids in Chinese waters.—Oceanologia et Limnologia Sinica. 13(2):202–204.

Department of Invertebrates, Museum of Comparative Zoology, 26 Oxford St., Cambridge, Massachusetts 02138, U.S.A.